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Main Manuscript title: Extinction of the Thylacine.

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Abstract

The Thylacine (*Thylacinus cynocephalus*), or 'Tasmanian tiger', is an icon of recent extinctions, but the timing of its final demise is shrouded in controversy. Extirpated from mainland Australia in the mid-Holocene, the large island of Tasmania became the species' final stronghold. Following European settlement, the Thylacine was heavily persecuted and pushed to the margins of its range. The last captive animal died in 1936, but numerous sightings were reported thereafter. Here we collate and characterize the type, quality, and uncertainty of over a thousand unique sighting records of Thylacines since 1910. We use this novel and unique curated database to underpin a detailed reconstruction and mapping of the species' spatio-temporal distributional dynamics, to pinpoint refugia of late survival and estimate the bioregional patterns of extirpation. Contrary to expectations, the inferred extinction window is wide and relatively recent, spanning from the 1980s to the present day, with extinction most likely in the late 1990s or early 2000s. While improbable, these aggregate data and modelling suggest some chance of ongoing persistence in the remote wilderness of the island. Although our findings for this iconic species hold intrinsic value, our new spatio-temporal mapping of extirpation patterns is also applicable more generally, to support the conservation prioritization and search efforts for other rare taxa of uncertain status.

Significance statement

Like the Dodo and Passenger Pigeon before it, the Thylacine has become an iconic symbol of human-caused extinction. Even today, reports of the Thylacine's possible ongoing survival in remote regions of Tasmania are newsworthy and continue to capture the public's imagination, with much debate over whether the extinction event has yet occurred and if so, when? We show, using a unique and robust spatio-temporal mapping and modelling approach, underpinned by the world's first sightings database (from 1910-present day), that the Thylacine likely persisted until the late 20th century, with some possibility of ongoing survival.

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Introduction

Prior to European settlement in the early 1800s, the large island of Tasmania supported a small but stable endemic population of this cursorial predator (1)—a 'marsupial wolf'—that had become extirpated on mainland Australia during the late Holocene, after surviving the earlier wave of Pleistocene megafaunal extinctions (2). Due to deliberate persecution (facilitated by government and private bounties), incidental snaring by fur traders, habitat modification and possibly disease (3), the Tasmanian population of Thylacine declined to extreme rarity by the early 20th century, with the last confirmed wild captures in the 1930s (4). The last captive Thylacine died in the Hobart Zoo on 7th September 1936, a date now commemorated annually as 'Threatened Species Day' in Australia. Fifty years later, in 1986, the species was formally designated as Extinct by the International Union for the Conservation of Nature. However, with many unconfirmed sightings reported in the decades following the 1930s (5), speculation has run rife that the Thylacine might have persisted far longer than formally accepted, in the wilderness of Tasmania. Indeed, as one of the most famous of recently 'extinct' species, and an archetype of convergent evolution (with placental canids) (6), a resolution of the details surrounding the final fate of the Thylacine holds great interest to both the public and to conservation science (7).

Apparently reliable sightings came from former trappers and bushmen through to the 1960s, and dedicated expeditions continued thereafter, including an intense localized search by authorities in 1982 following a highly rated sighting by a Parks ranger. The regularity and frequency of apparently plausible but unverified sightings reported over the last 84 years has not only raised the Thylacine to iconic status in the global public's eye, but also made it paradoxically challenging to scientifically reconstruct the timeline of its fate. In short, is the species extinct (and if so, when did it most likely occur), or are there grounds for the belief of ongoing persistence? Past efforts to prove the ongoing persistence of the Thylacine involved deliberate (albeit geographically restricted) field searches (8), sometimes financially motivated (e.g., media mogul Ted Turner offered a prize of $100 000 in 1983, and *The Bulletin* magazine of $1.25 million in 2005). More recently, mathematical models have been used, but their inferences are of questionable merit, being based on a highly simplified sighting record (one observation per year) or using generalizations from life-history correlates (9-11). Although statistical approaches for

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extinction inference have been developed recently to incorporate observation quality explicitly (12, 13), these could not be applied to the Thylacine because the sighting data were uncollated.

With the aim of resolving this intriguing historical-ecological conundrum, we developed a comprehensive, quality-rated database of post-bounty Thylacine sighting records from Tasmania and devised a novel spatio-temporal method to take explicit account of uncertainties to map its extinction dynamics. The sighting database was compiled by exhaustively searching for and cataloguing records from official archives, published reports, museum collections, newspaper articles, microfilm, contemporary correspondence, private collections or other miscellaneous citations and testimony. Each observation was dated, geotagged, quality-rated, categorized by type, and linked to image files of the original source material. Only post-1910 records were considered, being the period following the government bounty after which the species was considered rare (1). Records were classified as physical specimens, expert sightings, other observations, signs (e.g., tracks), and were all rigorously quality rated.

Results and Discussion

The final database comprised 1,237 entries (99 physical records, 429 expert sightings), with observations from all years except 1921, 2008 and 2013. Most records from 1910 to 1936 (the year the last captive specimen died—a male captured in 1931 (14), see photograph in Fig. 1) were of confirmed kills or live captures, although 56.6 % (128) of the 226 entries dating from this period were unverified sightings. The last fully documented wild animal (with photographs) was shot in 1930, but there is little reason to doubt the veracity of two bodies noted from 1933, nor the two capture-and-releases from 1935 and 1937. Thereafter, a further 26 deaths and 16 captures were reported (but not verified), along with 271 sightings by ‘experts’ (e.g., former trappers, bushmen, scientists or officials). The remaining 698 observations from Tasmania were made by the general public. There were notable spikes in reporting rates in 1937 and 1970, the former following legal protection and the latter arising from media attention linked to a well-publicized expedition. There are also many examples of discrete spatio-temporal sighting clusters with closely matching visual descriptions, the interrelationships of which would not have been apparent at the time the reports were submitted to authorities. Overall, the annual number of

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reports in the six decades spanning 1940–1999 were relatively constant ($\overline{x}$ = 14.9 year-1, $\sigma\overline{x}$ = 1.15), but fell substantially ($\overline{x}$ = 3.6, $\sigma\overline{x}$ = 0.60) from 2000–present. A breakdown of observations by type and quality, and time-series plots, are reported in the Supplementary Information.

The fate of the last individual of a species is rarely witnessed by human observers. This is especially the case for species like the Thylacine, which ranged widely but sparsely across large swathes of the Tasmanian wilderness. The last survivors were probably increasingly difficult to detect as they became ever more wary of people, as population size dwindled, and as the species' spatial distribution contracted and disaggregated (9, 11, 15). A direct reading of the physical evidence implies extinction in the wild by the late 1930s. However, when species are driven to extreme rarity, most of the final records will be uncertain sightings; in the case of the Thylacine, after securing legal protection in 1936, there was a disincentive to self-report kills, for fear of penalty or prosecution (9). Given these real-world complexities, what can be said about the true extinction date of the Thylacine? To tackle this problem, we applied a newly developed method for inferring the probability of persistence at any date beyond that of the final record under circumstances where most (or all) observations are uncertain but not equally reliable (16). This combines a probabilistic re-sampling of sighting records with a statistical extinction-date estimator (EDE): here we focus on two of the many possible EDE approaches; i) the optimal linear estimator model, used for famous examples such as the Dodo (*Raphus cucullatus*) (17), ii) the variable-sighting-rate method proposed by McInerny and colleagues (18). Both models are robust to cases where sighting frequency declines over time, and to sparse sighting records.

Restricting the EDE inference to only the physical specimens leads to an uncontroversial conclusion: extinction prior to 1940 (Table 1a). However, if unverified expert reports and other opportunistic sightings by the public are considered—down-weighted proportionally by their quality rating (see Methods)—the extinction window spans a later period, from the 1980s to the present, although the probability of ongoing persistence to 2020 is low (Table 1a, Fig. 1a,b). This might seem surprisingly recent, but is borne out by, for example, the search efforts from Parks & Wildlife authorities in the 1980s that were motivated by apparently highly credible sightings (19). A scenario-sensitivity analysis shows our results to be robust to permutations in the record-

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inclusion criteria or assignment of sighting probabilities (Fig. 1c). Although this new extinction-range estimate is much more recent than a previously published range (1936–1943) derived from a Bayesian model of mixed-certainty sightings (10), the latter result has been criticized for only using a small fraction (<10%) of all possible records and for being extremely insensitive to information embodied in the corpus of uncertain sightings (9).

The Tasmania-wide analysis (Table 1a) agglomerates sighting records of the Thylacine from across the island, irrespective of location. However, extinction often progresses via an intermediate process of range contractions and spatially heterogenous declines, themselves driven by a variable local intensity of threats like habitat change and hunting. One way to gain insight into the regional pattern of extirpations that typically precede global extinction is to disaggregate the sighting record into the Tasmanian ecozones (20). A corresponding analysis of bioregional clusters of sightings, based on EDEs fitted to the physical-specimen and expert-sightings data (Table 1b), reveals a general pattern of local losses starting in south-east and midland regions of the island (abutting areas where grazing, agriculture and settlement was concentrated) and later extending to the remote wilderness areas of the center and south-west. This results in a median extinction date of 1998, but the confidence intervals for these extirpations are wide for many ecozones, with all but two overlapping with the present day.

For greater spatial fidelity and a visualization of the dynamical time course of range decline for the Thylacine, we devised a novel algorithm for creating a geographical projection of point-wise extinction-date estimates on a 0.1° grid. To implement this, we down-weighted the contribution of records surrounding each landscape-grid point using a distance-decay function, while retaining each record's respective sighting probability, to produce a multi-weighted contour surface, superimposed on a map of Tasmania (details in Methods). The situation in 1937 (based on a mixture of records on kills, captures and expert sightings) was of a severe decline across most of the landscape, with pockets of probable persistence in south-central and north-west regions of the island, likely connected by dispersal corridors (Fig. 2a,b). There was also some possibility of a remnant isolated sub-population persisting in the north-east at that time, but with strong evidence for an early extirpation (by the 1920s) in the midlands and along the south-east

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coastal region, where the bounty killing had been particularly intensive (21). From 1938 onwards, all records (through to 2019) are of unverified sightings of varying quality, from experienced trappers to the naïve public, and including many apparently credible reports. These data (Fig. 2c,d) indicate extirpation by the early 1960s across most of the southern half of the state, with longer-term persistence along a band stretching across the Tasmanian Wilderness World Heritage Area, from Lake Pedder in the south-center across to the western edge of the central highlands and up to the Tarkine in the north-west. There is also remarkable congruency across the two sets of extirpation maps in the geographic location of potential refugia ('hotspots'), despite being based on assessment of completely temporally separate, non-overlapping data (the latter period has no certain, verified records). The most likely termination date for the species seems to have occurred within this zone by the late 1990s, although the upper confidence bounds of the model include the present day in some wilderness regions of the island.

Given the extensive sighting record that post-dates the death of the last captive individual—integrated using spatially explicit inferential methods that account for mixed-quality observations—it is reasonable to conclude that a cryptic, remnant population of the Thylacine persisted for many decades after the last captive animal died, perhaps even to the present day. Why then, was the species never detected by scientific field methods? Modern remotely triggered instruments are among the most cost-effective ways to record elusive vertebrate wildlife, and hidden cameras have been used to rediscover carnivore species thought extinct, like the Zanzibar leopard (*Panthera pardus adersi*) (22, 23). However, digital-trail-camera technology has only been widely deployed in Tasmania over the past two decades, with earlier visual searches and film-camera field operations being of relatively short duration and restricted geographical coverage (19). Our new method for mapping spatial contours of extirpation dates is useful not only for reconstructing the dynamics of the Thylacine's range contraction, but also for identifying and prioritizing the most likely spatial refugia of the species (should it persist). Indeed, the extirpation-mapping algorithm is general and could be applied equally to other species of conservation concern that are verified to survive but where the synthesis of sighting records (confirmed or uncertain) has previously defied integration. Additionally, these extirpation-probability maps could be unified with existing habitat- and climate- envelope methods (using known or inferred occurrences recorded prior to a species' decline), to pinpoint

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regions where both available niche space and recent sightings indicate potential survival, as a target for more intensified search efforts, restoration, or rewilding.

In sum, this collective body of evidence and associated analyses indicates that the continued persistence of the Thylacine is unlikely—but possible—and that the true extinction year, if the species is indeed now extinct, occurred much later than the commonly held date of 1936. Indeed, the inferred extinction window is wide and relatively recent, spanning from the 1980s to the present day, with extinction most likely in the late 1990s or early 2000s. While improbable, these aggregate data and modelling suggest some chance of ongoing persistence in the remote wilderness of the island. Although our findings for this iconic species hold intrinsic value, our new spatio-temporal mapping of extirpation patterns is also applicable more generally, to support the conservation prioritization and search efforts for other rare taxa of uncertain status (24-26).

Materials and methods

The approach involved the following steps: (i) collation and georeferencing of Thylacine sighting records from Tasmania into a database of unique observations; (ii) error-checking, attribute scoring, and quality-rating; (iii) application of 'extinction date estimators' (EDE), coupled with the weighted selection of sighting records, to infer the island-wide and regional distribution of times to extinction for the Thylacine; (iv) a sensitivity analysis on the impact on extinction time of bioregional disaggregation and lower record-inclusion probability; and (v) spatially continuous distribution mapping, illustrating the regional patterns of extirpation.

Database compilation and validation

We compiled and curated a comprehensive repository of documented Thylacine sighting records from Tasmania, covering the period from the year after the last Government bounty was paid, to the present (1910 to 2019). We refer to this as the Tasmanian Thylacine Sighting Records Database (TTSRD). By examining sources exhaustively, spanning official archives, published reports, past [partial] compilations of sighting records (1, 5, 19), museum collections, newspaper and media articles, microfilm, contemporary correspondence, private collections and other miscellaneous

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citations and testimony, we were able to amass 1,237 unique observations from this period, as well as resolving previous anomalies and duplications.

The TTSRD is presented in a flat-file format (.xlsx or .csv), with one observation per row, and column data for a unique ID, sighting location (with notes), date (year/month [or season]), geo-reference (latitude/longitude and a precision class), sighting type (kill, capture, expert or non-expert visual observation, secondary evidence) and quality-rating (a score between 1 [lowest] to 5 [highest], based on a subjective composite of information regarding the observer's credentials and experience, number of observers, context, and veracity of the description supplied), sighting meta-data (road or bush, driving or walking, day or night, near or far distance, number of observers, and number of Thylacines recorded), observer remarks/notes, and a reference and link to an image of its source material(s). Confidentiality requirements necessitated the redaction of names and addresses for 89 records, but efforts were made to prevent this censure affecting the essential content of the reports. The TTSRD was checked rigorously for duplicate and erroneous entries (e.g., there were examples when the year or location did not exactly match, or when observer's names were misspelled, but other corroborating or correlative evidence pointed to a duplication). Any errors found were archived and removed, with their unique ID not reused.

Extinction date estimation

Given the difficulties inherent in observing rare or critically endangered taxa, statistical methods (EDE) have been developed to *infer* probable extinction dates (or, by inversion, probabilities of persistence) from a time series of sighting records. Recent approaches to EDE have sought to incorporate a mixture of certain and uncertain sighting records (12). Both Bayesian (13, 24) and frequentist (16, 25) methods have been developed, each with advantages, limitations and differing philosophical framings of the problem. In this analysis, because of the character of the data embodied within the TTSRD, we chose to use a recently developed frequentist method for the inclusion and relative weighting of observations (16, 25), implemented in Program R (v4.0.2), because this approach can incorporate explicit sighting probabilities on uncertain data, multiple sightings within a year, and mixed records of variable type and quality. The method makes use of established frequentist EDE (18, 25, 26) for statistical inference, but probabilistically re-samples

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the observations of the full sighting record to generate a frequency distribution of extinction times. Like all frequentist EDE, the null hypothesis underlying the statistical inference is of persistence, with each sighting assigned a probability of being correct, given an assumption that the species persisted up to at least the point in time when the observation was made. (A detailed evaluation of the assumptions underpinning this approach, and the alternatives, are given in the Supplementary Information.)

Sensitivity analysis

A multi-scenario sensitivity analysis was done on inferences made by the EDE-model-under-uncertainty and is reported in Table 1, with details in the Supplementary Information. Therein, Table S3 gives the relative probability (P) weightings of records by type (physical specimen, expert observation, expert indicator of presence, other observations and other indicators), for low (L), default (D) and high (H) scenarios, and Table S4 reports the probability multipliers on the record weightings given in Table S3, which depend on the quality rating (QR) of the observation. Table S5 shows the results of scenarios for the date of extinction of the Thylacine in Tasmania, as per Table 1b, except based on all sightings rather than physical specimens and expert sightings only. Extinction-date inferences are given for individual bioregions, based on the combination of physical specimens and expert-sighting records (Table S6), for all available records (Table S7), and for physical specimens only (Table S8).

Spatial analysis

The last capture and the last confirmed kill of a Thylacine in the wild was located in a semi-agricultural region of north-west Tasmania. However, many reports continued to come thereafter from more remote central and south-west of the island, a vast stretch of wilderness that was sparsely settled and relatively rarely traversed or trapped. To capture this spatial pattern of regional extirpations (as a nearly inevitable prelude to global extinction), we used the Interim Biogeographic Regionalization of Australia (IBRA7) framework (20) as a basis for disaggregating the TTSRD records spatially into distinct Tasmanian bioregions. These are defined based on common climate, geology, landform, native vegetation, and species

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information. We then aggregated the smaller bioregions into four larger, spatially coherent clusters (*South-East* = Tasmanian Northern Midlands, Tasmanian South East; *North-East* = Ben Lomond, Furneaux; *North-West* = Tasmanian Northern Slopes, King; *West / World Heritage Area* = Tasmanian Central Highlands, Tasmanian West, Tasmanian Southern Ranges) and analyzed the Thylacine record collections separately for each cluster.

This basic biogeographic-based division of the full TTSRD has the advantage of permitting a semi-spatial breakdown of the sighting records into an ecologically meaningful regionalization—suitable for discrimination of discrete-spatial patterns of extirpation—whilst still yielding enough records for a statistically robust EDE-based inference. A limitation of this approach of biogeographic analysis is that it assumes implicitly that the sub-populations of Thylacine across regions follow independent fates (i.e., they are not interconnected by dispersal). In practice, although bioregional delineations like IBRA7 are intended to be ecologically consistent, their boundaries typically do not constitute landscape-scale barriers.

To create a visualization of the extirpation pattern and relax the 'hard-boundary' assumption inherent in the approach based on bioregional divisions, we developed a novel, spatially continuous mapping method, implemented algorithmically in R. The input is a raster map of grid cells representing the landscape occupied by the species. In our case, we gridded the main island of Tasmania into 69,562 × 0.01° longitude-latitude cells (~ 0.92 km^2 within the Tasmanian latitudinal range of -40.65 to -43.64° S). For each grid cell, a subset of sighting records within a pre-defined orthodromic distance are selected (we chose a threshold of 75 km for the Thylacine in Tasmania). Sighting records within that subset are then weighted for inclusion in the probabilistic EDE based on a distance-decay function. We used a truncated exponential model, $w = \min(1, ab^{-d})$, where $a = 2.15$, $b = 1.074$ and d is the distance (in km) from the target cell (other mathematical models could be used, if deemed more appropriate to a situation). This choice of parameter values led to a weighting (w) of 1 for all records within 10 km distance, declining to approximately 0.5 by 20 km, 0.25 by 30 km, 0.05 by 50 km, and 0.01 by 75 km. For use in the EDE, the w value of each record is multiplied by its sighting probability (see above, 'Extinction date estimation' section). Because of the large number of grid cells, we used the analytical version of the McInerny el al. EDE model-under-record-selection-uncertainty (18), as derived in

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(16) and modified from (25), as this is more computationally efficient (it required no re-sampling). This was iterated over all spatial-grid cells to produce the final map of inferred extirpation times. For enhanced execution speed, the R code makes use of multi-core parallel processing.

The obvious advantage of this innovation is that it generates a continuous (smoothed) geographic surface of extirpation times that can be visualized (see Fig. 2), based on the inferred year of extinction as derived from an EDE. Because the method makes use of all records within a defined radius (with their selection probability down-weighted monotonically by distance), it does not impose hard boundaries like in the discrete-bioregional approach, and captures spatial-pattern information from both *within* and across the bioregions. Moreover, regions of high uncertainty (wide confidence bounds) are readily distinguished (and visualized) from those underpinned by more data and/or better-constrained inferences on extirpation. The main limitation is that the mathematic form (and parameter values) of the distance-decay function is ultimately arbitrary, yet these choices strongly determine the degree of spatial smoothing apparent in the resultant probability map. Although the spatially continuous mapping algorithm was developed specifically for the Thylacine, the approach (and R code) is designed to be general and could be readily applied to other species which have a sufficient number of geo-referenced sighting records.

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(https://github.com/bwbrook/ttsrd), along with The Tasmanian Thylacine Sighting Records Database (TTSRD) as CSV file or a Microsoft Excel workbook, and images (attachments).

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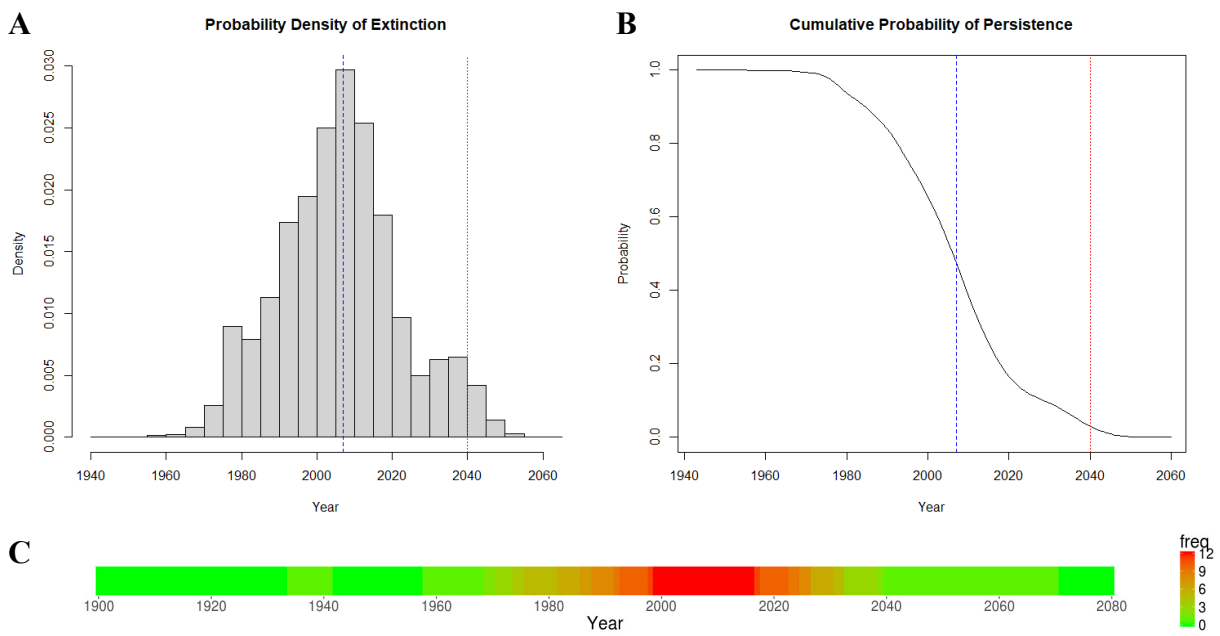

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Fig. 1. Simulated extinction dates for the Thylacine in Tasmania, using all 1,237 quality-rated sighting records. **A**. Probability-density distribution of the inferred extinction date from the optimal linear estimator, based on probabilistic re-sampling of all 1,237 specimen and observational records from 1910–2019, with the low scenario for probability weightings on the uncertain records. **B**. Cumulative probability of persistence at a given calendar year, as derived from the distribution shown in **A**. In each panel, the blue and red vertical lines show the mean time of extinction and upper 95% confidence bound, respectively. **C**. Sensitivity heatmap, a merger of upper/lower -bound weights assigned to the sighting-type probabilities (default/conservative): physical records = 1/1, expert observations = 0.25/0.05, expert indications (e.g., footprints, scats) = 0.1/0.01, other observations = 0.05/0.005, other indications = 0.01/0.001. Photograph is of the last captive Thylacine, taken on 19th December 1933 at the Hobart Zoo by zoologist David Fleay (image courtesy David Fleay trustees).

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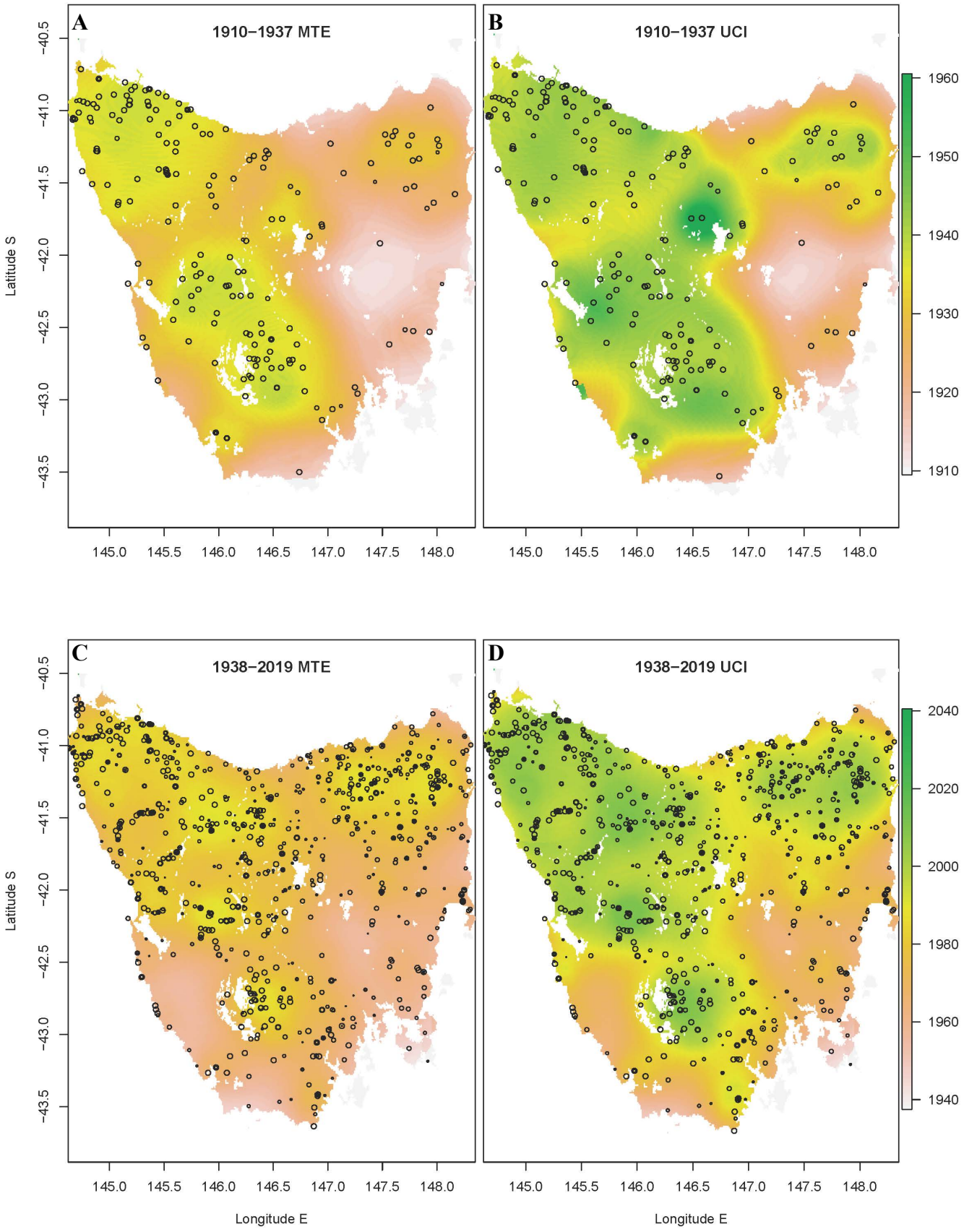

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Fig. 2. Spatial extirpation pattern for the Thylacine in Tasmania. Colored contour maps of the inferred year of local extirpation, estimated for each pixel across a 0.1° geographical grid of the island (area = 64,519 km^2). The results were generated by fitting a re-sampled (16) extinction-date estimator model (18) to records down-weighted by sighting uncertainty and distance from the target pixel (see Methods). **A**. mean time of extinction (MTE) and **B**. upper confidence interval (UCI) for records spanning 1910–1937 (a mix of verified and uncertain records, n = 258). **C**, **D**, as for A, B, except using only records from 1938 onwards (all uncertain records, n = 979). The circles in each plot show individual sightings, sized based on their rated quality: 5 (highest quality) for the largest circles, down to 1 (lowest) for the smallest.

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Table 1. Scenarios for the date of extinction of the Thylacine in Tasmania. **A**. Assessment using an aggregate of records from across the island, from 1910–2019, based on verified physical specimens only, unverified expert sightings only, or all record types (including physical records, expert sightings, and other observations by the public, weighted by the record's quality rating using default or low assigned probabilities). **B**. Spatially disaggregated scenarios, using records specific to four main bioregions, based on physical specimens and expert sightings only. Shown for each scenario is the number of records sampled (n), mean time of extinction (MTE, calendar year) and the 95% confidence intervals of the simulations (95% CI, based on distribution percentiles), and the modelled probability of extinction in the year 2020 (PE-2020) (16). The two alternative statistical extinction-date estimators, used for inference of extinction date based on sightings records, are those of McInerny et al. 2006 (18) and Roberts & Solow 2003 (17).

		McInerny et al. 2006			*Roberts & Solow 2003*		
Scenario	n	MTE	95% CI	PE-2020	MTE	95% CI	PE-2020
A. Tasmania-wide							
Physical specimens only (P)	99	1937	1934–1938	1	1939	1935–1940	1
Expert sightings (E; unverified)	429	2002	1986–2015	1	2006	1987–2023	0.806
All records (default weights)	1237	2011	1997–2019	>0.999	2016	1999–2026	0.598
All records (low weights)	1237	1994	1970–2018	0.986	2007	1975–2040	0.834
B. Bioregional (P & E records)							
South-East	24	1972	1920–1997	1	2012	1925–2132	0.657
North-East	68	1985	1970–1996	1	1993	1971–2018	0.980
North-West	167	1991	1972–1998	1	2001	1977–2015	>0.999
West / World Heritage Area	264	1999	1978–2015	1	2008	1983–2031	0.794

Footnote. The IBRA7 Bioregions (20) included within each geographic aggregation of sighting records are as follows: South-East = Tasmanian Northern Midlands, Tasmanian South East; North-East = Ben Lomond, Furneaux; North-West = Tasmanian Northern Slopes, King; West / World Heritage Area = Tasmanian Central Highlands, Tasmanian West, Tasmanian Southern Ranges.